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## INTROGRESSION OF *ALNUS SERRULATA* AND *ALNUS RUGOSA*

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In the eighth edition of Gray's Manual of Botany, two species of alders in the subgenus *Alnus* are indicated as occurring in New Hampshire, each of which has a variety and several forms. The two species are distinguished as follows: *Alnus rugosa* (Du Roi) Spreng. has leaves with a rounded base, ovate or elliptical in shape with a tendency to be broadest below the middle, doubly-toothed leaf margin, strong veins on the green lower surface, prominent lenticels on the stems, and nutlets and bracts with a characteristic shape. Its variety *americana* (Regel) Fern. differs in having leaves glaucous rather than green underneath. *Alnus serrulata* (Ait.) Willd. has leaves with angled or cuneate base, obovate and broadest above the middle, a margin almost singly toothed, weak or vanishing veins on the green or glutinous lower surface, inconspicuous lenticels, and nutlets and bracts differing from *A. rugosa* in a way to be stated later. Its variety *subelliptica* Fern. has broader leaves, although still broadest above the middle, and a rounded leaf base.

The present study was started when the writer became interested in the northern limits of the ranges of these two species and their varieties in New England. *A. rugosa* var. *americana* is a well-marked variety occurring throughout northern New England and extending north to Labrador. Fernald (1945) states that this variety is decidedly more northern in range than var. *rugosa*. An investigation of the range of the latter from herbarium sheets presented some

difficulties. The question of whether leaves are glaucous or green can only be determined from mature leaves and in natural light. Under these conditions, if the observer has had some practice, the distinction is readily apparent. Many of the herbarium specimens were collected in April when there were no leaves, so that the distinction can not be made. In other cases, the specimens were mounted in such a way that it was possible to examine the lower surfaces of the leaves. Subsequent field observations indicate that the new leaves of var. *americana*, as they appear in June are green; by early July they become glaucous. Alder typically grows in swamps or open low land; when it grows in shady environments the leaves are thin and pale green with the glaucous character barely discernible. The material on some sheets that were labeled var. *rugosa* was of uncertain identity. Altered notations on many sheets indicated confusion of *A. serrulata* with *A. rugosa* var. *rugosa*.

In Tamworth, New Hampshire, *A. rugosa* var. *americana* is common in open moist habitats. These plants are quick to invade a poorly-drained hayfield and are also common along streams. *A. serrulata* is near its northern limit in Tamworth and is confined to shores of lakes and occasionally along edges of rocky streams. Some plants occur that can be referred to *A. rugosa* var. *rugosa*. These, however, although having green leaves which set them off from var. *americana* are not readily distinguishable from *A. serrulata*. As the scope of this investigation was broadened to include the whole state of New Hampshire, this situation was observed to be characteristic. It seemed probably that hybridization and introgression were going on between *A. rugosa* var. *americana* and *A. serrulata* producing a mixed assemblage of plants, some of which could be referred to var. *rugosa*.

To investigate this situation, it was decided to study populations and analyze them by pictorialized scatter diagrams of the type devised by Anderson (1949, 1952, 1953). Characters to be used were based on leaves, lenticels, and fruit. As there is considerable variation in leaves on sterile plants, especially on young shoots, only leaves on fruiting branches were used. Preferably these were collected after the middle

of July when the fruit was mature. An alder colony typically consists of a number of separate clumps of plants, which, judging from the variation that occurs, are clonally distinct, although it is possible that in some cases a new clump could arise from a rootstock. In a colony extending for a distance of two or three hundred feet, many plants may not fruit, so the sampling consisted of collecting branches from available fruiting plants that appeared to be separate. Leaves on fruiting branches are typically quite small. Where possible a branch was collected with at least one undamaged leaf six to eight centimeters in length. Lenticel type is significant, and, as collection of bark is difficult, the character of the lenticels was noted at the time. Notches were then cut on the branches in accordance with a standardized code; three notches indicating prominent lenticels, two indicating that some were indefinite, and one indicating the lenticels were indistinct.

Seven characters were scored including most of those used by Fernald in the eighth edition of Gray's Manual. The angle at the base of the leaf was measured on a 15° degree sector scale.

Single as opposed to double serration was determined by counting the major teeth on one leaf margin using certain "typical" leaves from well marked samples of the two species as standards for comparison.

The character of the lower surface of the leaves, ranging from glutinous to glaucous, was determined by examining the leaves in daylight and again comparing with standards. Usually the distinction between green and glaucous was obvious, but where the glaucous character could barely be discerned, the leaves were marked pale. Sometimes it appeared as if the leaves were glaucous because of disease.

To measure whether the leaf was broadest above or below the middle, it was placed on graph paper and the broadest point determined. The distance from this point to the midpoint of the leaf was divided by half the length of the leaf to form the "midratio". This was taken as positive if the broadest point was above the middle and negative if it was below.

Lenticels, especially on larger stems, are usually prominent in the case of *A. rugosa* var. *americana* and indistinct

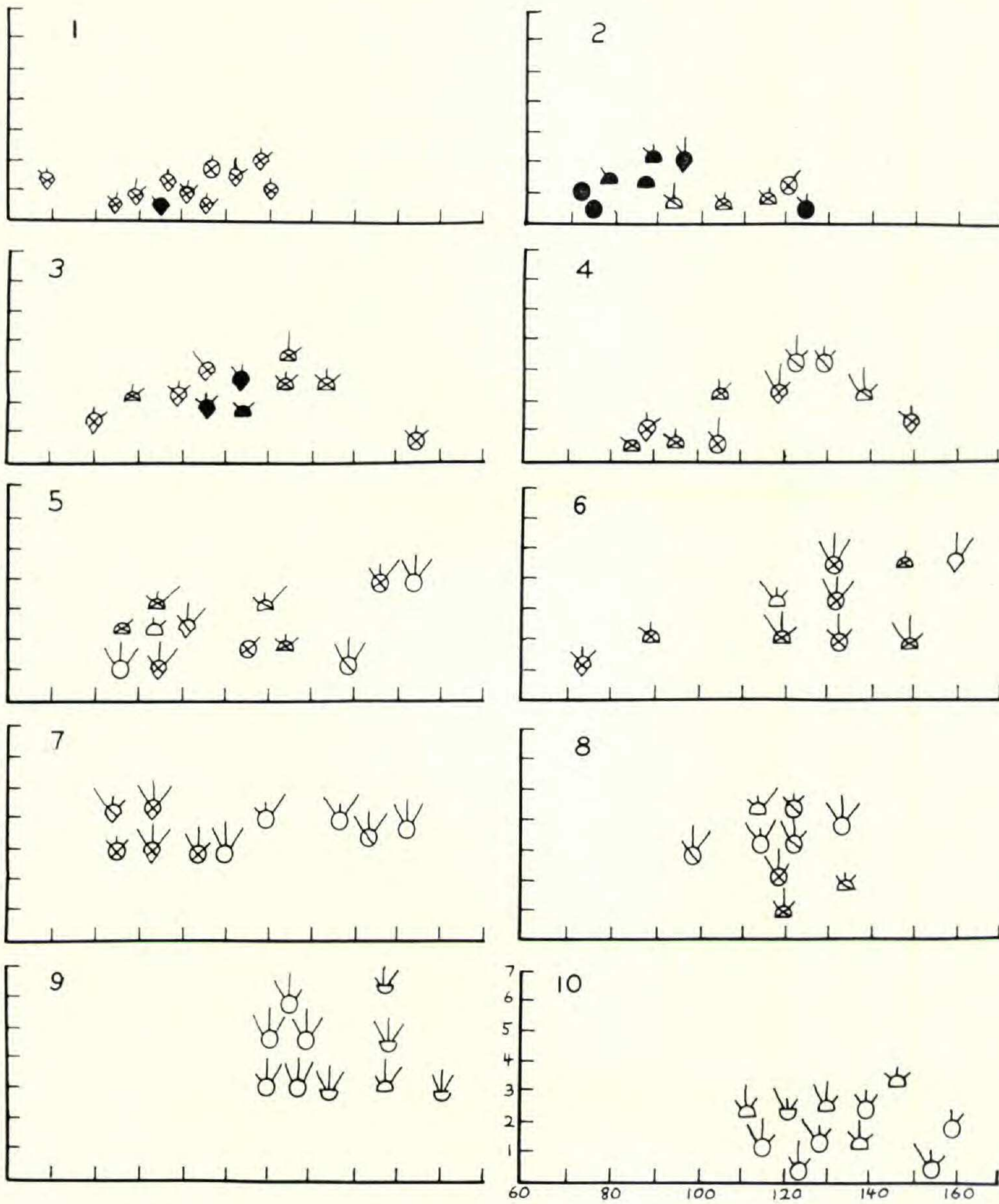
in the case of *A. serrulata*. The lenticel character was recorded at the time of collection as indicated above.

Veins on the lower surface were ranked as prominent, intermediate or vanishing. This character was somewhat variable, but well-marked trends were apparent. The leaves were compared with characteristic leaves of *A. serrulata* and of *A. rugosa* var. *americana* and rated according to which one of the two they most nearly approached.

Well developed nutlets and bracts of the two taxons seemed to be markedly different. The bracts of *A. serrulata* have a lower portion with straight narrow sides with the upper portion rather abruptly flaring; the bracts of *A. rugosa* var. *americana* have the lower portion with diverging sides, with the upper portion less distinct. Nutlets of var. *americana* tend to be rhombic with the top portion triangular. Nutlets of *A. serrulata* are obovate with prominent shoulders at the top. These differences become apparent when the fruit is mature; about the middle of July in New Hampshire. On the diagrams the fruit is labeled broad if the nutlets and bracts resemble var. *americana*; narrow if they resemble *A. serrulata*.

Some fifty populations were sampled from different areas of New Hampshire and northern Massachusetts, with an effort made to sample different environments. Then populations believed to be typical of the situation are shown in Figures 1 - 10. Following Hardin (1957), intermediates are labeled "species A" × "species B", while apparent back crosses are labeled as "species A" (× "species B") indicating that "species B" contributed the minority of the genes. Figure 1 from a swamp shows typical *A. serrulata*. Figure 2 from a lake shore shows *A. serrulata* near the northern limit of its range where much *A. rugosa* var. *americana* is present. It appears to be good *A. serrulata* but may not be genetically pure. Figure 3 from a swamp shows *A. serrulata*

FIG. 1-10. Pictorialized scatter diagrams showing introgression between *A. serrulata* and *A. rugosa* var. *americana*. All collections by the author. 1. *A. serrulata* (Boxford, Mass.). 2. *A. serrulata* (Tamworth, N. H.). 3. *A. serrulata* (× var. *americana*) (Hampton, N. H.). 4. *A. serrulata* (× var. *americana*) (Freedom, N. H.). 5. *A. serrulata* × var. *americana* (Hampton, N. H.). 6. *A. serrulata* × var. *americana* (Freedom, N. H.). 7. *A. rugosa* var. *americana* (× *A. serrulata*) (Tamworth, N. H.). 8. *A. rugosa* var. *americana* (× *A. serrulata*) (Milton, N. H.). 9. *A. rugosa* var. *americana* (Sandwich, N. H.). 10. *A. rugosa* var. *americana* (Ossipee, N. H.).



EXPLANATION OF SYMBOLS

ABSCISSA	ANGLE AT BASE	ORDINATE	NUMBER OF TEETH
MIDRATIO	LEAF COLOR	LENTICELS	VEINS
+ .2	GLAUCOUS	PROMINENT	STRONG
+ .1	PALE	WEAK	WEAK
0	GREEN	VANISHING	VANISHING
- .1	GLUTINOUS	FRUIT	
- .2		BROAD	
		INTERMEDIATE	
		NARROW	

modified by genes from var. *americana* and contains three plants in the upper right of the diagram that could be called var. *rugosa*. Figure 4 from a sandy lake shore also shows modification of *A. serrulata* by genes from var. *americana*. In this case some of the plants might be referred to *A. serrulata* var. *subelliptica*. Figure 5 from a swamp and Figure 6 from a lake shore show populations about intermediate between *A. serrulata* and var. *americana*. Figure 7 and Figure 8 both from swamps show var. *americana* modified somewhat by *A. serrulata* and include plants that could be referred to var. *rugosa*. Figure 9 from a poorly drained field shows good var. *americana* unmodified by any *A. serrulata*. Figure 10 from the edge of an acid peat bog shows var. *americana* apparently modified by the acid environment. The leaves are smaller and the major teeth less prominent.

TABLE 1

TAMWORTH			FREEDOM		
Plant No.	Leaf angle	Width/length	Plant No.	Leaf angle	Width/length
1	75	.45	1	90	.65
2	75	.5	2	105	.6
3	90	.5	3	105	.7
4	90	.6	4	120	.6
5	90	.7	5	120	.75
6	105	.7	6	120	.8
7	120	.6	7	135	.7
8	120	.7	8	150	.8

These populations are apparently typical of the alder situation, judging from field studies in northern New England and herbarium studies for the whole area in eastern North America. *A. rugosa* var. *americana* is a distinct taxon with constant characteristics, especially in the northern part of its range where no *A. serrulata* is present. *A. serrulata* is a distinct species, with a range more southern than that of var. *americana*, extending north to north-central New Hampshire and central Maine. When the two taxa occupy the same area, introgression occurs producing intermediates, and plants that approach one or the other of the supposed parent. These intermediates do not seem to demand any particular hybridized environment, although they normally

occur in places that may be regarded as somewhat intermediate, and that have almost invariably been disturbed by man. Plants close to var. *americana* but green underneath could be referred to var. *rugosa*; however, these usually are variable and resemble *A. serrulata* in some respects.

The key characters that distinguish var. *subelliptica* from var. *serrulata* are leaves gradually rounded at base as opposed to cuneate or subacute, and broad leaves with a width-length ratio of .6 to .9 as opposed to narrower leaves with a ratio of .35 to .65. Width to length ratios were measured for a number of populations. Table 1 shows some typical results. Var. *subelliptica* appears to be one extreme of the normal variation of *A. serrulata* populations, although in some cases these populations may be modified by gene flow from var. *americana*. There is no indication that var. *subelliptica* is a geographic variety.

There are various named forms of both species and varieties, some of them depending on pubescence of lower surfaces of leaves. Many populations of both species had leaves varying from glabrous to varying degrees of pubescence. *A. serrulata* forma *nanella* is described as a dwarf shrub with small leaves and aments. Alders growing in adverse environments, such as peat bogs or silty shores of rivers are frequently stunted. *A. serrulata* forma *emarginata* has emarginate leaves. It is not infrequent to find an alder with some of the leaves emarginate.

In conclusion it appears that in the subgenus *Alnus*, in the northeast, the two good native taxa are *A. serrulata* and *A. rugosa* var. *americana*. The latter can readily be distinguished by the glaucous character of the lower surface of the mature leaves. Any plant with this trait, if not diseased, will possess the other characteristics of the taxon. Plants with deep green or glutinous leaves and cuneate leaf bases will possess the specific characters of *A. serrulata*. These two taxa hybridize and backcross frequently, the resulting gene exchange producing a variable assemblage of plants including some intermediates that would be referred to *A. rugosa* var. *rugosa*.

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SOME NEW OR OTHERWISE INTERESTING REPORTS  
OF LILIACEAE FROM THE SOUTHEASTERN STATES<sup>1</sup>

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Several interesting plants in the Liliaceae have been found as a consequence of field work in the southeast. As might be expected, this family is one of the best represented ones in our herbaria, but it is still incompletely known.

One of these collections consisted of several specimens of *Aletris* collected by Dr. W. H. Duncan of the University of Georgia. Dr. Duncan found both white- and yellow-flowered *Aletris* plants growing in approximately equal numbers in the same population in Chatham Co., Georgia, and they appeared at first to be plants of *A. farinosa* L. and *A. lutea* Small, respectively.

Since perianth color and shape are the two most important characteristics for specific separation in the North American species of *Aletris*, the identifications appeared to be obvious. However, upon closer examination, it was discovered that in neither of these types was there semi-epigyny, one of the

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